

Maintenance of melanism in the spider *Pityohyphantes phrygianus*: is bird predation a selective agent?

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The sheetweb spider *Pityohyphantes phrygianus* (Araneae: Linyphiidae) exhibits a continuous variation in dark colouration due to polygenic inheritance of the trait. There are three main phenotype classes: pale, intermediate and melanic. In natural populations, the proportion of melanics seems to be stable at a low frequency, usually 3–4 per cent. An hypothesis about possible selective differences between melanics vs. non-melanics was evaluated in a 2-year field experiment. Bird predation was prevented in a large number of spruce branches, the natural habitat of the species, by means of coarse-meshed nets. The experimental branches and the controls were sampled four times (spring and autumn in 2 years). Bird predation was shown to affect negatively the spider abundance. Removal of bird predation increased the *P. phrygianus* mean density between 2.3 and 10.5 times the control density. However, no difference in the proportion of melanics in experimental vs. control branches could be established. It is suggested that bird predation is not a major selective force affecting the phenotype proportions. Hence, the mechanism of maintenance of melanism in natural populations of *P. phrygianus* is unclear, but some alternative explanations are discussed.

Keywords: bird predation, colour variation, melanism, natural selection, *Pityohyphantes phrygianus*, spider.

Introduction

Arthropod populations which exhibit intraspecific variation in colouration are often subject to strong predation pressure. The different phenotypes may be vulnerable to visual predators in relation to their conspicuousness. The maintenance of colour polymorphism has often been attributed to frequency-dependent predation. Visual predators tend to take the common morph disproportionately often and thereby maintain the polymorphism by apostatic selection (Allen, 1988; Endler, 1988).

The habitat in which the arthropods live is also important. A classical case of melanic phenotypes involves the peppered moth *Biston betularia* in Britain. Kettlewell (1973) and others showed that birds may act as important selective agents affecting the frequencies of the moth phenotypes (reviews in: Lees, 1981; Brakefield, 1987; Berry, 1990). The relative frequencies of the moth morphs, especially the *carbonaria* and *typica* phenotypes, that were chosen by birds depended on the background colour. Thus, due to crypsis, the phenotypes that matched the background colour of the

habitat were favoured. Consequently, predation pressure may explain differences in morph frequencies between sites and may also be an important clue in explaining the maintenance of colour polymorphism in this species as phenotype fitness varied between sites. However, the results concerning the bird predation effects on *B. betularia* have been questioned (Mikkola, 1984), and a pilot experiment showed that, depending on resting position on the trees, the results may change quantitatively but probably not qualitatively (Howlett & Majerus, 1987). Selection due to agents other than visual predators should be invoked in order to understand the dynamics of the colour polymorphism in *B. betularia* (Brakefield, 1987). Berry (1990) listed a number of factors which are poorly understood, e.g. effects due to dispersal, non-avian predators, the niche of *betularia*, and other non-visual effects on fitness differences between the morphs.

Vertebrate predators that hunt visually are known to exercise a strong influence on the abundance of spiders in many contrasting habitats, e.g. Scandinavian coniferous forest (Askenmo *et al.*, 1977; Gunnarsson, 1983), small, vegetated sandy islands of the Bahamas

(Schoener & Toft, 1983; Spiller & Schoener, 1988), xeric hardwood in Netherland's Antilles (Pacala & Roughgarden, 1984) and riparian woodland in Arizona (Riechert & Hedrick, 1990). Such predation pressure may theoretically be a strong selective force. Thus, bird predation has been suggested to be a selective agent involved in the maintenance of colour polymorphism in two spider species: the sheetweb spider *Pityohyphantes phrygianus* (Gunnarsson, 1987a) and the Hawaiian happy face spider *Theridion grallator* (Gillespie & Tabashnik, 1990). However, in neither of these species has evidence for an effect of bird predation been presented. Here, the author reports an extensive field experiment which was performed to elucidate the effects of bird predation on *P. phrygianus*.

P. phrygianus is restricted to coniferous forests and it is a common species on spruce branches (*Picea abies*) in southern Sweden. This sheetweb spider has a skewed primary sex ratio (Gunnarsson & Andersson, 1992) and after severe winters the proportion of males may be very low since these are more susceptible to cold-induced mortality than are the females (Gunnarsson, 1987b). The life-cycle is biennial and in their second winter both sexes actively forage in late autumn and on mild winter days, resulting in a considerable weight increase (Gunnarsson, 1988). A continuous variation in dark colouration was observed in a population in south-west Sweden (Gunnarsson, 1985) and similar colouration differences between individuals have been observed in many populations in southern Sweden (personal observation). Crossing experiments between the three main phenotype classes — pale, intermediate, melanic — revealed a polygenic inheritance and the narrow heritability was estimated as 0.43 (Gunnarsson, 1987a). A small-scale laboratory experiment showed that the propensity to move at low temperature was higher for melanics than for pale plus intermediate phenotypes (Gunnarsson, 1987a). The author suggested that the profits of increased activity, i.e. more time available for winter foraging, may be counterbalanced by increased bird predation. This may explain the low frequency, about 4 per cent, of melanics in the study population (Gunnarsson, 1987a). Experiments by Avery & Krebs (1984) have shown that spiders which are moving frequently experience a higher risk of being eaten by birds than do specimens which are more sedentary.

To test the prediction that melanic spiders are more often taken by bird predation than are non-melanics, the author conducted a large-scale field experiment. Spruce branches were enclosed in net-sacks that prevented bird predation but permitted migration of spiders and their prey. Samples from experimental and control branches were taken at regular intervals. The

data were analysed in order to establish whether: (i) bird predation significantly affects the *P. phrygianus* population; and (ii) the proportion of melanics was higher in branches where bird predation was excluded than otherwise.

Materials and methods

The experimental site was part of a large coniferous forest situated about 40 km east of Göteborg, south-west Sweden. Spruce (*Picea abies*) was the predominant tree species, but there were also scattered stands of pine (*Pinus sylvestris*) and birch (*Betula* spp).

In spring 1989, the study was started in an approximately 2 ha experimental area. The experimental trees were randomly selected and included if the following two conditions were fulfilled: (i) the height of the tree was not lower than 8 m; and (ii) branches were available in all directions. On each tree, two controls and two experimental branches were selected randomly at 1.5–4 m above the ground. The experimental branches were enclosed with coarse-meshed nets (mesh size 10 mm) that prevented birds from foraging on the branches except from the outside on parts close to the net. The spiders and their prey, however, were free to move within and between branches. In addition, about one-third of the needles was artificially removed on one control and one experimental branch in each tree. This treatment was made for other experimental purposes, i.e. investigating the effects of vegetation structure on the spider community (to be reported elsewhere).

The density of *P. phrygianus* on branches where needles were experimentally removed and branches with the natural needle density were compared. Net-enclosed branches and those without netsacks were analysed separately. Since branches within a tree were compared, this permitted a statistical test for related samples (Siegel & Castellan, 1988). There were no statistically significant differences between the branch categories in pairwise comparisons (Wilcoxon signed ranks test, $0.94 > P > 0.11$), except in one case. Among net-enclosed branches in spring 1991, the mean density on needle-thinned branches was about twice the density on branches with natural needle density ($P = 0.015$). The reason for this is unknown. Consequently, in the analysis of bird predation effects in spring 1991, the experimental branches protected from bird predation comprised those branches with natural needle density only (this procedure was conservative and hence the bird predation effect may be underestimated).

Starting in autumn 1989, samples were taken among the experimental trees four times: late September to

early October 1989; mid to late March 1990; late September to early October 1990; and mid to late March 1991. At each sampling occasion, the trees were taken at random among the experimental trees selected previously. If one or more of the four branches had been destroyed, the tree was omitted from the sample. The branches were cut into plastic sacks which were sealed and brought to the laboratory where they were stored at 4°C until examination. Each branch was cut into pieces and carefully examined over a white bowl (see Askenmo *et al.*, 1977; Gunnarsson, 1983 for details). Spiders were preserved in 70 per cent ethanol. The branches were dried at 85°C for 24 h and their dry mass recorded. Densities are given as number of spiders per dry branch-mass (cf. Gunnarsson, 1990). Additional spiders were collected from non-experimental trees at each sampling occasion (except in autumn 1990) on about 50–75 branches. This was necessary because of the low frequency of melanic spiders in the population (Gunnarsson, 1987a), and the low density on unprotected branches (see Results). The needle-carrying parts of branches were enclosed in a plastic sack and then the branches were shaken vigorously (Gunnarsson, 1988). The *P. phrygianus* specimens were sorted out immediately and preserved in 70 per cent ethanol.

The specimens were classified as melanic or non-melanic (i.e. pale plus intermediate) phenotypes. Melanics were defined as individuals with an area of 70 per cent, or more, dark colouration on the abdomen (Gunnarsson, 1985, 1987a). This is an arbitrary classification since there is a continuous variation in the dark colouration of *P. phrygianus*. However, as judged by the human eye, the lower bounds represents the transition from a lighter to a clearly blackish phenotype. Some credence to the classification of phenotypes was given by a behavioural difference in activity between melanics and non-melanics at low temperatures (Gunnarsson, 1987a).

Results

The effects of bird predation were analysed by comparisons of spider density between the experimental branches (protected against foraging birds) and the controls. In the four comparisons made, i.e. two autumn and two spring samples, the density of sub-adult *P. phrygianus* was significantly higher on the experimental branches than on untreated controls (Fig. 1).

In the autumn samples, the mean densities on experimental branches were 2.6 times the mean density on controls in 1989 (Mann-Whitney *U*-test; z (corrected) = -3.66, $N_1 = N_2 = 30$, $P = 0.0002$) and

2.3 times the controls in 1990 (z (corr.) = -2.88, $N_1 = N_2 = 30$, $P = 0.0039$). The spring samples revealed an even stronger bird predation effect. In spring 1990, the mean density of experimental branches was 10.5 times the mean on controls (z (corr.) = -6.95, $N_1 = N_2 = 36$, $P < 0.0001$). The spring sample in 1991, showed that the mean density on experimental branches was 4.1 times the mean on controls (z (corr.) = -4.10, $N_1 = 30$, $N_2 = 15$, $P < 0.0001$). Thus, the experimental results showed that visual predators, in this case passerine birds, exercise a strong predation pressure on *P. phrygianus* in all seasons in the author's experimental area.

In comparisons of the percentages of melanics in experimental and control branches, the sample size of the control was increased by random sampling on non-experimental trees. This resulted in sample sizes between 100 and 206 in the control group. The number of spiders obtained on experimental branches was between 102 and 304. However, the autumn 1990 sample was not possible to analyse with statistical methods. In this autumn, the densities of *P. phrygianus* were much lower than in any other sampling period in both experimental and control branches (Fig. 1), and no melanics at all were found in either category of branches (Table 1).

The frequency of melanics did not differ significantly between the branches in which bird predation was excluded and the controls in any of the three comparisons made (Table 1). In autumn 1989, the frequency of melanics was very low, 1.0 per cent, in the natural population. Excluding bird predation resulted in a small, non-significant, increase to 3.1 per cent melanic specimens. Comparisons between experimental branches and controls in the spring samples did not reveal any trend in the proportion of melanics. In 1990, the melanic percentages were similar: 3.6 per cent in experimental branches vs. 3.0 per cent in control. In 1991, the frequency of melanics in the experimental branches was 2.0 per cent, and 4.8 per cent in the control branches.

Discussion

The aim of the present study was to test whether melanic and non-melanic spiders differ in their susceptibility to bird predation. However, the relevance of the experiment depends on a number of conditions that must be fulfilled. First, birds must hunt for spiders and be able to affect the populations numerically. Such effects have been verified by earlier experiments in the present study area (Askenmo *et al.*, 1977; Gunnarsson, 1983). Secondly, birds must hunt visually to be able to distinguish between melanic and non-melanic spiders.

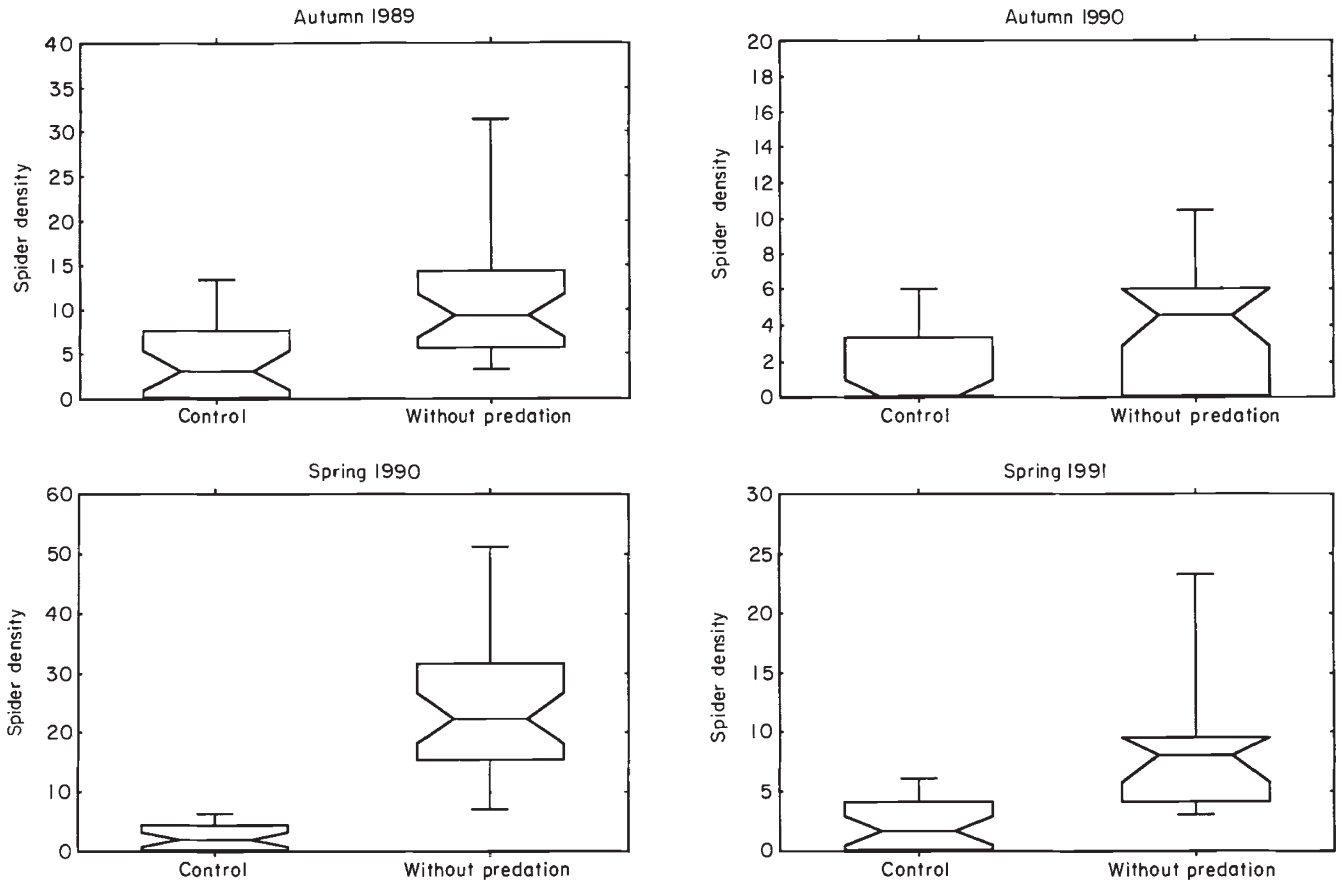


Fig. 1 Effect of bird predation on *P. phrygianus* abundance on spruce branches. Density is given as number of spider per kg branch-mass (dry weight). Each sampling consisted of: (i) unprotected control branches; and (ii) experimental branches without bird predation due to net-enclosing. The box-plots show the median and the 10th, 25th, 75th, and 90th percentiles for each sample. The notches represent 95 per cent confidence intervals about the median. N.B. Different scales on y-axis.

Table 1 Numbers of melanics and non-melanics on control and on experimental branches — protected from bird predation — in four samples. No melanics were recorded in the autumn sample in 1990. Difference in the proportion of melanics in control branches vs. experimental branches was tested by Fisher's exact test

Year, Season	Control branches (C) Melanics/non-melanics	Experimental branches (E) Melanics/non-melanics	Total	(C) vs. (E)
1989, autumn	2/204	5/158	369	$P = 0.25$
1990, spring	3/97	11/293	404	$P = 0.99$
1990, autumn	0/23	0/46	69	—
1991, spring	5/99	2/100	206	$P = 0.44$

There is no doubt that birds use visual signals when hunting and that they constitute a considerable potential as selective agents on different organisms (e.g. Endler, 1991). It is known that birds have a greater ability than humans to detect moving objects, but as birds see ultraviolet light their pictures of natural

objects should be different from ours (Waldvogel, 1990). Thirdly, given the points above, it must be shown that there is a strong predation pressure on the species studied and not only on spiders in general. The results from the field experiment are conclusive. The density of *P. phrygianus* in branches protected from

bird predation was 2.3 to 10.5 times higher than on controls. Thus bird predation is potentially a very strong selective agent on sub-adult specimens of *P. phrygianus*.

In *P. phrygianus*, the frequency of melanics is usually only 3–4 per cent in natural populations (Gunnarsson, 1987a). This means that there may be problems, due to sampling error, in establishing changes in the proportion of melanics. With this in mind, it is important for the interpretation of the results to know the magnitude of change in the population that it was possible to detect in the experiment. Given the sample sizes in experimental and control branches, the frequency of melanics in the experimental population was changed to produce statistically significant differences compared with the observed frequency of melanics in the control, i.e. the natural population. In autumn 1989, the melanic frequency was 1.0 per cent in the controls. There would have been a significant difference if the frequency of melanics was 4.5 per cent in the experimental branches. In the spring samples, the melanic frequencies in the controls were 3.0 and 4.8 per cent, respectively. A significant increase in the proportion of melanics had to be 9.2 and 12.7 per cent in protected branches, i.e. by factors of 3.1 and 2.7, respectively. These frequencies suggest that changes in the proportion of melanics by factors between 2.7 and 4.5 may be detected whereas smaller frequency changes will not be revealed.

I assumed that the migration rates of melanics to and from the experimental, i.e. net-enclosed, branches were balanced. During mild winters, with a high number of days available for activity and foraging (Gunnarsson, 1988), melanic spiders are probably more active than non-melanics at low temperatures (Gunnarsson, 1987a). However, since both experimental winters were much milder than usual in south-west Sweden, the average activity levels may have been higher than normal and some migration probably occurred. High spider activity during winter may reduce the probability of detecting frequency differences among the phenotypes in the experiment. A higher activity than normal may select against melanics if: (i) black spiders are easier to detect than non-melanics; and (ii) the probability of a specimen being detected and eaten by a bird increases. However, the data on the melanic frequency in the natural population in autumn, 1.0 per cent, compared with spring values, 3.0 per cent and 4.8 per cent, suggest that the effect of a mild winter is of minor importance in this case.

In the experimental branches, the net *per se* introduced a new structure to the branches that may increase the number of web sites and/or hiding places and promoting higher spider abundance. However,

birds may forage also on net-enclosed branches by taking spiders close to the net since bills of passerines easily penetrate the net with 10 × 10 mm mesh size. Tits (*Parus* spp) were observed to visit the net-enclosed branches in the experimental site. Moreover, the net is a rather simple structure compared to the spruce branches, which are characterized by having a fractal dimension, and spider abundance is positively correlated with complicated plant structures (Gunnarsson, 1990, 1992). Thus the effect on spider density by the net itself may be negligible.

In conclusion, the experimental results provide evidence for a strong bird predation pressure on *P. phrygianus* populations. However, it appears that such predation is of minor importance as a selective agent on melanic vs. non-melanic spiders, at least under the prevailing conditions during the present study.

There are several possible explanations for the absence of bird predation effects on phenotype frequencies. First, if apostatic selection alone is maintaining the colour variation at a low equilibrium frequency and this selection pressure is removed, then the trait would be neutral, and no rapid change in the proportion of melanics is expected. Secondly, the activity difference between melanics and non-melanics observed at low temperatures (Gunnarsson, 1987a) may not be valid when predators are present. For instance, the spiders may register that a bird is close by branch vibrations and change their behaviour, i.e. the spiders may then hide quickly. Thirdly, perhaps the melanic spiders are more cryptic on the branches than are the non-melanics. Fourthly, the experimental winters were much milder than normal in south-west Sweden. It is not known whether the birds, mainly *Parus* spp and gold-crest *Regulus regulus*, change their foraging behaviour in response to winter severity but their population dynamics is clearly related to ambient temperature in winter (Ekman, 1984).

An alternative hypothesis not involving differential predation is that weak selection, e.g. due to a climate gradient, is involved in maintaining the colour variation in *P. phrygianus*. This appears to be the case in the spider *Enoplognatha ovata*, a polymorphic species with three main colour morphs — *lineata* (plain yellow), *redimita* (yellow with two red stripes), and *ovata* (red dorsal surface). The colouration is controlled by three alleles at one locus, and involves a dominance hierarchy between the alleles (Oxford, 1983). Field experiments have failed to uncover any strong selection on the morphs at a local level (Oxford & Shaw, 1986; Reillo & Wise, 1988a). The morph-frequency patterns in *E. ovata* support an hypothesis of a weak, or intermittent selection on the morphs, possibly correlated with climatic factors. This seems to apply both to

UK (Oxford, 1985; Oxford & Shaw, 1986) and North America (Reillo & Wise, 1988b; Reillo, 1989). Recently, Oxford (1991) reported frequencies of colour morphs in allopatric and sympatric populations of *E. ovata* and *E. latimana* (Hippa & Oksala, 1982), a sibling species exhibiting some of the same morphs as *E. ovata*. In his analyses, Oxford (1991) found no correlation between the morph proportions in sympatric populations of the two species in some sites in Wales and he concluded that stochastic events may be important in controlling morph frequencies but locally acting species-specific selection could not be excluded entirely.

The maintenance of melanism in *P. phrygianus* is still an unsolved problem. However, almost nothing is known about spatial variation in the frequencies of the main phenotype classes. Future studies on geographical clines and phenotype frequencies in coniferous forests with different environmental conditions may be important to test alternative hypotheses.

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